HOLOCENE CHANGES IN THE FLORA OF RAGGED TOP, SOUTH-CENTRAL ARIZONA

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ABSTRACT

A total of 73 plant taxa were identified from three packrat (*Neotoma* sp.) middens radiocarbon dated between 14,550 and 5020 yr B.P. from Wolcott Peak in Ragged Top, Pima County, Arizona. Most (80.1%) of the plants still grow in the area although only 17.8% still occur at the midden site. Fourteen late Wisconsin woodland/chaparral species (19.2%) were locally extirpated in the Holocene. Today five (6.5%) occur in nearby (<5 km), five in moderately distant (<40 km), and four (5.5%) in more distant (90–135 km) mountain ranges. *Agave deserti* was associated with *Juniperus osteosperma, Opuntia whipplei,* and *Pinus monophylla* in the late Wisconsin but their ranges no longer overlap. The Ragged Top flora shifted composition in the Holocene as woodland species died out and Sonoran desertscrub species arrived at different times. Relict populations of *Quercus turbinella, Vauquelinia californica,* and *Yucca baccata* reflect cooler, winter-rainfall ice age climates prior to about 8900 years ago. Isolated populations of *Echinopepon wrightii, Ipomoea cristulata,* and *Pisonia capitata* were likely established by chance seed dispersals 4000 to 8900 years ago in more subtropical climates of the middle Holocene.

Seeds, fruits, leaves, twigs, and spines preserved in ancient packrat (*Neotoma* sp.) middens have provided a rich fossil record for plants that grow on rocky slopes in the North American deserts for the last 40,000 years (Van Devender et al. 1987). In the Sonoran Desert, woodlands dominated by *Pinus monophylla* (singleleaf pinyon), several species of *Juniperus* (junipers), and *Quercus turbinella* (shrub live oak) descended to 600 m elevation, about 600 m lower than modern woodlands, during the Wisconsin glacial period (>43,000 to about 11,000 years ago; Van Devender 1990). A xeric woodland with *J. californica* (California juniper), *Yucca brevifolia* (Joshua tree), and *Larrea divaricata* Cav. (creosotebush) occurred down to about 300 m. Desertscrub dominated by *L. divaricata* and *Ambrosia dumosa* (white bursage) were likely to have been present in lower areas along the Colorado River throughout the Pleistocene (Cole 1986; Van Devender et al. 1990).

After about 8900 years ago in the middle Holocene, desertscrub communities developed in the northeastern Sonoran Desert in Arizona. The last woodland/chaparral plants moved upslope as important Sonoran species including *Carnegiea gigantea* (saguaro), *Cercidium floridum* (blue paloverde), and *Encelia farinosa* (brittlebush) returned from their ice age refugia, presumably in Sonora,

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Mexico. Relatively modern Sonoran desertscrub communities did not form until about 4000 years ago in the late Holocene with the arrival of *C. microphyllum* (foothills paloverde), *Stenocereus thurberi* (organpipe cactus), and other more subtropical desert species.

In the northeastern Sonoran Desert in Arizona, the landscape is a mosaic of mountain ranges adjacent to broad valleys, or emergent from desert plains. Mountain slopes typically support rich mixed desertscrub dominated by *Carnegiea gigantea* and *Cercidium microphyllum* while sparse lowland communities are dominated by *Larrea divaricata* (Shreve 1964; Turner and Brown 1982). Species that live in rocky habitats often have discontinuous distributions restricted to the mountains. Some of the isolated populations are plants typically found in woodland, chaparral, or more subtropical desertscrub (Brown 1978) that may reflect favorable climates in the past or chance dispersals. Our survey of the flora of Ragged Top, a rugged desert peak in the northeastern Sonoran Desert, yielded a number of interesting isolated plants (Wiens 1990). In an attempt to understand the developmental history of the Ragged Top flora and to provide insight into the timing of isolation of the relicts, we examined the plant macrofossils in packrat middens from Wolcott Peak, a secondary peak in Ragged Top. Here we present the results of those analyses and discuss their biogeographical implications.

Study Area

Geology. Ragged Top is a steep, rugged desert mountain in Pima County, Arizona, approximately 6.5 km north of Silver Bell and 50 km northwest of Tucson (Fig. 1). It is bordered on the east and north by Avra Valley and on the west and south by the Silver Bell Mountains, a desert range, composed of Cretaceous volcanics and granodiorite, reaching 1300 m elevation. Ragged Top rises to 1190 m while Wolcott Peak on the southeast side reaches 1015 m (Fig. 2). The north and east slopes of Ragged Top are middle Precambrian granite, while the south and west bajadas are mainly Quaternary alluvium and talus. The range itself is composed of a deeply weathered ridge of Tertiary intrusive rhyolite which is mostly oriented east to west (Nowlan et al. 1989). North–south fractures and subsequent weathering have formed many small clefts and deep canyons. Packrat middens were found preserved in the dry crevices and rockshelters.

Climate. The climate of Ragged Top is characteristic of the northeastern Sonoran Desert, with infrequent winter freezes, hot summers, and biseasonal rainfall (Sellers and Hill 1974; NOAA 1980). During summer, equatorial heating strengthens the subtropical Bermuda High moving moist air masses both westward from the Gulf of Mexico across the continent and north-northeastward from the Gulf of California in a pronounced summer monsoon. In winter,

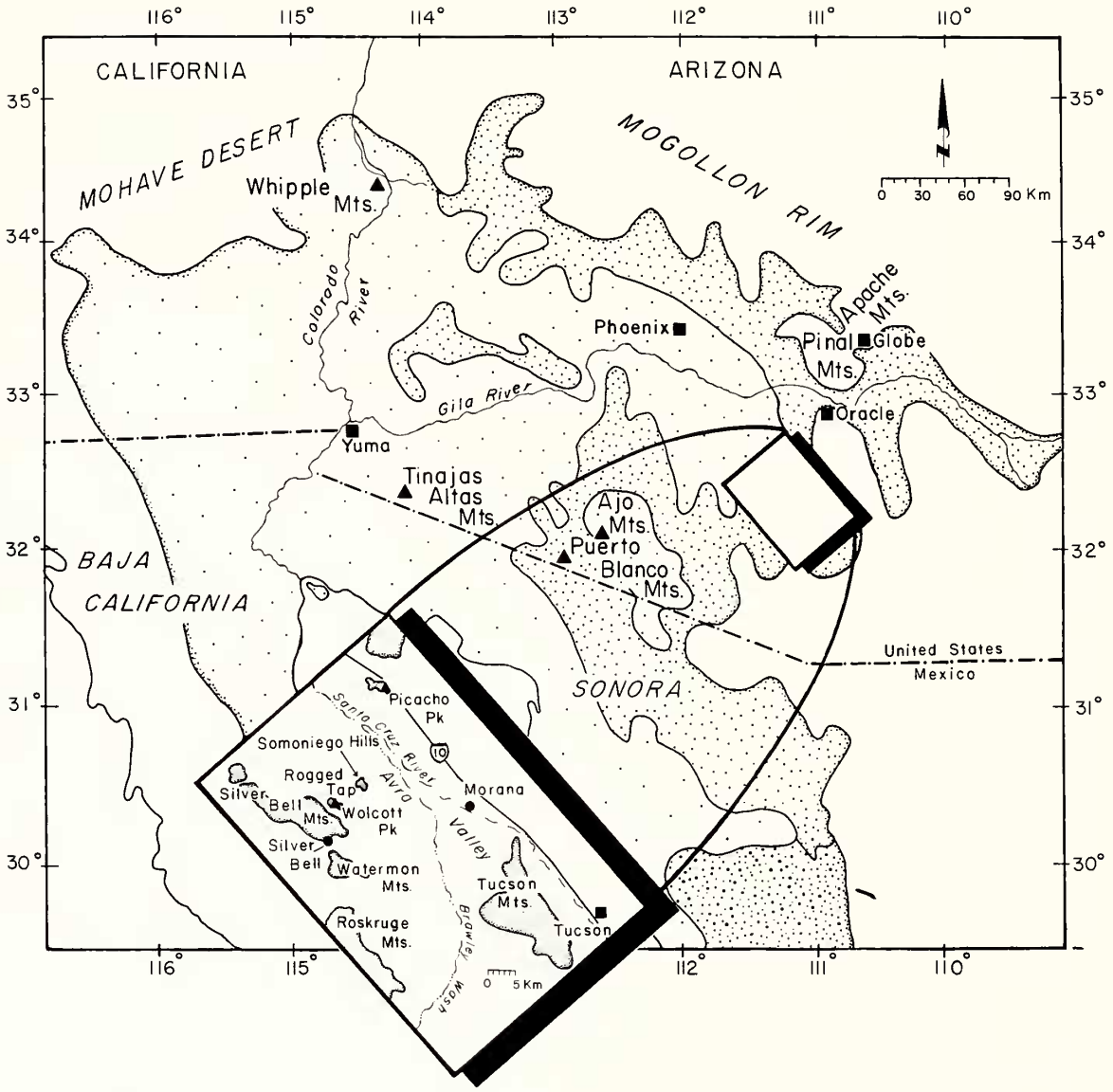

FIG. 1. Map of the study area. Arizona Upland subdivision of Sonoran Desert in heavy stipple; Lower Colorado River Valley in light stipple.

precipitation arrives from frontal storms moving east from the Pacific Ocean. The mean annual precipitation for Silver Bell at 825 m elevation is 312 mm/yr with 51.3% falling from July through September. Mean temperatures are 27.4°C annual, 17.3°C for January, and 37.3°C for July.

Vegetation. Ragged Top is in the Arizona Upland subdivision of the northeastern Sonoran Desert (Shreve 1964; Turner and Brown 1982). The desertscrub on the lower bajada is dominated by *Cercidium microphyllum, Ambrosia deltoidea* (triangleleaf bursage), and *Carnegiea gigantea* in association with *Cercidium floridum, Olneya tesota* (ironwood), and *Prosopis velutina* (velvet mesquite) along major washes. On steep, south-facing slopes *Encelia farinosa* (brittlebush) is also important. *Acacia greggii* (catclaw acacia), *Celtis pallida* (desert hackberry), and *Lycium berlandieri* (wolfberry) are common

A.

B.

FIG. 2. A. View of the southern slopes of Ragged Top and Wolcott Peak from the Silver Bell Mountains. B. View of study area from southeast. Typical Arizona Upland desertscrub in foreground with *Carnegiea gigantea, Cercidium microphyllum,* and *Fouquieria splendens.*

at cliff bases near the midden sites in association with *Acacia constricta* (whitethorn acacia), *Ambrosia ambrosioides* (canyon ragweed), *Fouquieria splendens* (ocotillo), *Horsfordia newberryi* (yellow felt plant), *Hyptis emoryi* (desert lavender), *Larrea divaricata, Simmondsia chinensis* (jojoba). Succulents include *Carnegiea gigantea, Ferocactus wislizeni* (fishhook barrel), and a variety of *Opuntia* spp. (chollas and prickly pears).

The north-facing slopes and canyons of Ragged Top provide mesic microhabitats. Shady, cool vertical cliffs, often more than 30 m tall, shelter *Brickellia californica* (brickell bush), *Celtis pallida, Eriogonum fasciculatum* (California buckwheat), *Forestiera shrevei* (desert olive), *Opuntia chlorotica* (pancake prickly pear), *Prosopis velutina, Quercus turbinella, Vauquelinia californica* (Arizona rosewood), *Yucca baccata* var. *brevifolia* (Schott) Benson & Darrow (banana yucca). Most of these are relict species more typical of desert grassland and chaparral communities at higher elevations.

In Avra Valley at the lower end of the bajada, the vegetation changes to a xeric desertscrub characteristic of the Lower Colorado River Valley subdivision. Dominants include *Larrea divaricata, Ambrosia dumosa, Olneya tesota, Hymenoclea salsola* (cheesebush), and, in grazed areas, *Isocoma tenuisecta* (burroweed).

Packrat middens. Packrats or woodrats are medium-sized rodents in the genus *Neotoma* (Cricetidae) that collect various plant materials for food and construction of a house or den (Finley 1958). When packrats live in dry rockshelters, urination perches in the dens can become indurated by urine into hard, dark, organic deposits termed middens. Plant remains in such middens provide excellent samples of the local vegetation within about 30 m of the rockshelter filtered through a packrat's dietary preferences and collecting habits.

When middens are carefully collected from discrete stratigraphic units and outer surfaces are removed, contamination is not a serious problem. Improvements in sampling and radiocarbon dating methods in the last 20 years have reduced contamination to a minimum. Radiocarbon dates on very small samples using the tandem accelerator mass spectrometer permit the antiquity of or contamination by individual species to be verified (Van Devender et al. 1985).

Methods

The Wolcott Peak samples were collected in 1971 before standard procedures to prevent contamination were developed (Van Devender 1973). Samples were collected from crevices at 860 m elevation facing south (WP2) and southwest (WP4, WP5). In the WP2 sample, several small chunks of midden from a deep narrow cleft were combined because of their similar appearance and unusual abundance of bone (Van Devender and Mead 1978; Mead et al. 1983). Midden

debris from the WP2 yielded an age of 5020 ± 80 yr B.P. (A–1216, radiocarbon years before 1950), several thousand years younger than expected for a juniper assemblage from a desert site. A separate date of 14,550 ± 800 yr B.P. (A–1286) on juniper twigs confirmed mixing of material of different ages. Radiocarbon dates on the other samples were: WP4: 5350 ± 100 yr B.P. (A–1236 on midden debris) and WP5: 12,130 ± 500 yr B.P. (A–1287 on *Juniperus* twigs).

Midden samples were disaggregated in water, washed through a 20 mesh soil sieve, air dried, and sorted under a binocular microscope. Plant specimens were identified using reference specimens in the Herbarium and the Desert Laboratory at the University of Arizona. Distributions for extralocal species were determined using specimens in the Herbarium and the literature. Plant fragments were ranked in an internal relative abundance scale ranging from rare to abundant: i.e., a single specimen ranked 1, the most common taxon 5, the remainder in between. More elaborate quantitative methods using percentages of identified specimens greatly increase the analytical effort without significantly improving the final result (Spaulding et al. 1990; Van Devender 1990).

The modern flora above 720 m elevation was surveyed briefly in 1971 and intensively from 1987 through 1992. Vouchers of modern plant specimens were deposited into the herbaria at the Arizona–Sonora Desert Museum and the University of Arizona. Species encountered near the midden sites are presented in Table 1. Plant nomenclature follows Lehr (1978) with authorities for exceptions given in the text or tables.

Results and Discussion

The plant macrofossils from the packrat middens provide glimpses of the flora and vegetation of Wolcott Peak at two times in the past, and help understand the history and development of a complex flora. A total of 73 plant taxa, including trees and woody shrubs (19.2%), subshrubs (9.6%), succulents (13.7%), herbs (41.2%), and grasses (16.4%) were identified from the three midden assemblages (Table 1). The number of taxa identified per midden ranged from 11 to 54 (av. = 35.7).

Late Wisconsin. The mixed WP2 assemblage yielded several typical woodland plants including *Berberis* sp. (barberry), *Juniperus erythrocarpa* Cory/*J. monosperma* (redberry/oneseed juniper), *J. osteosperma* (Utah juniper), and *Pinus monophylla.* Considering that these species are typical of late Wisconsin midden assemblages in the northeastern Sonoran Desert (Van Devender 1990; Anderson and Van Devender 1991; Van Devender et al. 1991), they were probably associated with the 14,550 yr B.P. date rather than the 5020 yr B.P. middle Holocene date.

TABLE 1. PLANTS IDENTIFIED FROM THE SITE AND IN PACKRAT MIDDENS FROM WOLCOTT PEAK, PIMA COUNTY, ARIZONA. Relative abundances: 1 = rare, 2 = uncommon, 3 = common, 4 = very common, 5 = abundant. Distribution codes: n = present at the midden site, WP = elsewhere on Wolcott Peak and surrounding bajada, RT = not on Wolcott Peak, but elsewhere on Ragged Top, SH = Samaniego Hills (4.5 km NE), SB = Silver Bell Mountains (3.5 km S), WM = Waterman Mountains (10 km S), TM = Tucson Mountains (35 km SE), e = extralocal, no longer in the nearby ranges. * = species in a midden sample; ka = thousands of years (radiocarbon dates in text).

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/ 5.0 ka)	WP4 (5.3 ka)
Trees and shrubs						
**Acacia greggii*	Catclaw acacia	Leaflets, thorns	3		2WP	
**Berberis* sp.	Barberry	Seeds, leaflets			2e	
**Celtis pallida*	Desert hackberry	Seeds, fruits, leaves	2	3n	3n	2WP
Cercidium microphyllum	Foothills paloverde		3			
**Condalia warnockii*	Mexican crucillo	Seeds		2RT		
Crossosoma bigelovii	Rhyolite bush		2			
**Encelia farinosa*	Brittlebush	Achenes	5	2n	2n	1n
**Eriogonum fasciculatum*	California buckwheat	Leaf		1WP		
Horsfordia newberryi	Yellow felt plant		2			
Hyptis emoryi	Desert lavender		2			
**Juniperus erythrocarpa* Cory/ *monosperma*	Redberry/oneseed juniper	Seeds, twigs		5e	5e 3e	3e
**Juniperus* cf. *osteosperma*	Utah juniper	Seeds, twigs				
Larrea divaricata Cav.	Creosotebush		3			
Lycium berlandieri	Wolfberry		3			
**Lycium* sp.	Wolfberry	Seed, twig		2n		
Olneya tesota	Ironwood		2			
**Pinus monophylla*	Singleleaf pinyon	Nuts, needles		2e	2e	
**Prosopis velutina*	Velvet mesquite	Mesocarps, leaflets		1WP	2WP	

Table 1. Continued.

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/ 5.0 ka)	WP4 (5.3 ka)
**Quercus turbinella*	Shrub live oak	Acorns, leaves, twigs		3WP	2WP	
**Rhus* cf. *aromatica* Ait.	Skunkbush	Seeds		2TM		
Simmondsia chinensis	Jojoba		4			
**Vauquelinia californica*	Arizona rosewood	Fruits, leaves		3RT		
			n = 11	11	9	3
Subshrubs and woody vines						
Bebbia juncea	Sweetbush		1			
**Abutilon incanum/malacum* Wats.	Indian mallow	Seeds, carpels		2WP	2WP	
**Brickellia* cf. *coulteri*	Brickell bush	Involucres, twig	2	1n	2n	
**Carlowrightia arizonica*		Capsule			1WP	
Cynanchum arizonicum (Gray) Shinners	Milkweed vine		1			
Ditaxis lanceolata (Benth.) Pax & Hoffman	Lanceleaf ditaxis		2			
**Ericameria cuneata*	Cuneate turpentine bush	Involucres, leaves, twigs		4n	1WP	1WP
**Ericameria laricifolia*	Turpentine bush	Leaf, twig	3	2n		
Eriogonum wrightii	Wild buckwheat		3			
Eupatorium solidaginifolium	Boneset		1			
Galactia wrightii			1			
Galium stellatum	Desert bedstraw		3			
Gymnosperma glutinosum	Tatalencho		2			

Table 1. Continued.

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/ 5.0 ka)	WP4 (5.3 ka)
**Janusia gracilis*	Desert vine	Fruits			2WP	
**Plumbago scandens*	Leadwort, hierba de alacran	Fruit			1WP	
Stephanomeria pauciflora	Desert straw		1			
Trixis californica			3			
			n = 12	4	6	1
Succulents						
**Agave* cf. *deserti*	Desert agave	Leaves, hooks		3WM	1WM	
**Carnegiea gigantea*	Saguaro	Seeds	2	2n	2n	5n
Echinocereus nicholii	Golden hedgehog		3			
**Ferocactus cylindraceus* (Engelm.) Orcutt	California barrel cactus	Seeds		2SH		
**Ferocactus wislizeni*	Fishhook barrel cactus	Seed	1	1WP		
**Mammillaria grahamii*	Fishhook pincushion	Seeds	1		2WP	
**Opuntia acanthocarpa*	Buckhorn cholla	Seeds	2	2WP	2WP	
**Opuntia bigelovii*	Teddy bear cholla	Seed	3		1n	
**Opuntia chlorotica*	Pancake prickly pear	Seeds	1	4WP	3WP	2WP
**Opuntia phaeacantha*	Variable prickly pear	Seeds		2WP	5WP	2WP
Opuntia cf. *spinosior* × *versicolor*	Hybrid cholla		1			
**Opuntia* cf. *whipplei*	Whipple cholla	Seeds		1e	2e	
			n = 8	8	8	3
Grasses						
Aristida adscensionis	Six-weeks threeawn		3			

Table 1. Continued.

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/ 5.0 ka)	WP4 (5.3 ka)
Aristida parishii/purpurea	Threeawn		2			
**Bouteloua barbata*	Six-weeks grama	Floret			1WP	
**Bouteloua curtipendula*	Sideoats grama	Florets			1WP	1WP
**Bouteloua* cf. *repens*	Slender grama	Florets			2RT	
**Brachiaria arizonica* (Scribn. & Merr.) S. T. Blake	Arizona panicgrass	Florets		2WP	2WP	
**Bromus carinatus*	Arizona brome	Florets		2WP		
Bromus rubens	Red brome		3			
**Digitaria cognata* (Schult.) Pilg.	Fall witchgrass	Florets		2WP		
**Eriochloa acuminata* (Presl.) Kunth.	Cupgrass	Floret			1SB	
**Hordium pusillum*	Little barley	Florets		2TM		
**Panicum hirticaule*	Witchgrass	Florets		2WP	2WP	
Poa bigelovii	Bigelow bluegrass		3			
Schismus barbatus	Mediterranean grass		3			
**Setaria leucopila*	Bristlegrass	Florets	3	4n	4n	2WP
**Stipa speciosa*	Desert needlegrass	Floret		1RT		
Vulpia octoflora	Six-weeks fescue		3			
**Vulpia* sp.	Fescue	Floret		1WP		
			n = 7	8	7	2
Herbaceous perennials						
**Ambrosia confertiflora*	Slimleaf bursage	Burs		2RT		
**Anemone tuberosa*	Windflower	Seeds		2WP		
**Artemisia ludoviciana*	White sage	Leaves		2SB		
Ayenia filiformis			2			

Table 1. Continued.

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/ 5.0 ka)	WP4 (5.3 ka)
**Cirsium* sp.	Thistle	Achenes, phyllaries		2TM		
**Datura wrightii* Regel	Sacred datura	Seeds		3TM		
Herissantia crispa			2			
Mirabilis bigelovii	Wishbone bush		3			
**Nicotiana trigonophylla*	Desert tobacco	Fruits	2		2n	
Notholaena standleyi	Standley cloak fern		2			
Penstemon parryi	Parry penstemon		3			
Siphonoglossa longiflora			1			
**Solanum elaeagnifolium*	Horse nettle	Seed		1SB		
**Tragia* sp.	Noseburn	Seeds		2WP		
			n = 7	7	1	0
Perennial/annual herbs						
**Allionia incarnata*	Trailing four o'clock, windmills	Seeds			2RT	
**Castilleja/Orthocarpus*	Indian paint brush/owl clover	Seeds		2WM		
Ditaxis neomexicana (Muell.-Arg.) Heller			1			
Eriogonum abertianum			3			
**Eriogonum inflatum*	Desert trumpet	Fruit			1WP	
Euphorbia arizonica	Spurge		3			
**Euphorbia melanadenia*	Spurge	Seeds, fruits		2RT	2RT	
Phaseolus filiformis	Bean		2			
**Physalis* sp.	Ground cherry	Seeds		2WP	2WP	

Table 1. Continued.

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/ 5.0 ka)	WP4 (5.3 ka)
**Sphaeralcea* sp.	Globe mallow	Carpels		2WP	2WP	
Verbena gooddingii	Vervain		3			
**Verbena* sp.		Nutlet			1WP	
			n = 5	4	6	0
Annuals						
**Amsinckia tessellata*	Fiddleneck	Nutlets		2WP		1WP
Antirrhinum nuttalianum	Snapdragon		2			
**Boerhavia erecta* L. var. *intermedia* (Jones) K. & P.	Spiderling	Fruits		2WP	2WP	
**Boerhavia wrightii*	Spiderling	Fruit			1RT	
**Bowlesia incana*	Hairy bowlesia	Seeds	2			2WP
Camissonia californica			2			
Camissonia chamaenerioides	Long-capsule primrose		3			
Caulanthus lasiophyllus (H. & A.) Payson			3			
Chenopodium neomexicanum	Fishy goosefoot		4			
**Cryptantha barbigera*	Bearded nievitas	Nutlets		2WP		
**Daucus pusillus*	Wild carrot	Mericarps	2	2WP	2WP	
Descurainia pinnata	Tansy mustard		2			
Draba cuneifolia	Whitlow grass		1			
Erodium cicutarium	Filaree		2			
**Erodium texanum*	Stork's bill	Seed		1WP		
Eucrypta chrysanthemifolium	Torrey eucrypta		4			
Eucrypta micrantha	Smallflower eucrypta		3			
**Euphorbia revoluta*	Spurge	Seed		1WM		
Filago californica			2			

Table 1. Continued.

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/ 5.0 ka)	WP4 (5.3 ka)
**Galium aparine*	Bedstraw	Seed		1WP		
Gilia stellata			2			
**Kallstroemia* sp.	Summer poppy	Seeds, leaves		4WP	2WP	
**Lupinus* sp.	Lupine	Seeds		2WP		
Malacothrix clevelandii			2			
Oenothera primiveris	Large yellow desert primrose		1			
Parietaria hespera	Pellitory		2			
Perityle emoryi	Rock daisy		1			
Phacelia crenulata	Caterpillar weed		3			
Phacelia distans	Caterpillar weed		2			
**Phacelia* sp.	Caterpillar weed	Seeds				2n
Pholistoma auritum			2			
**Plagiobothrys arizonicus*	Bloodweed	Nutlet		1RT		
**Plantago fastigiata* Morris	Indian wheat	Seeds		2WP		
Senecio lemmoni	Grounsel		2			
Silene antirrhina	Sleepy catchfly		3			
Spermolepis echinata	Scaleseed		2			
Steptanthus carinatus	Silver bells		2			
Stylocline micropoides	Desert nest straw		3			
**Thysanocarpus curvipes*	Lacepod	Fruit	3	1WP		
Vicia ludoviciana	Vetch		2			
			n = 28	12	5	2
			Total = 78	54	42	11

The 12,130 yr B.P. sample yielded remains typical of a late Wisconsin pinyon–juniper–oak woodland/chaparral dominated by *Juniperus erythrocarpa/J. monosperma, Ericameria cuneata* (cuneate turpentine bush), and *Opuntia chlorotica,* in association with *Pinus monophylla, Quercus turbinella, Rhus* cf. *aromatica* Ait. (skunkbush), *Vauquelinia californica,* and *Agave* cf. *deserti* (desert agave). Leaves originally reported as *Q.* cf. *emoryi* (Emory oak) and *Rhamnus crocea* (hollyleaf buckthorn) in Van Devender (1973) were reexamined and found to be within the range of variation of *Q. turbinella.* Considering the Holocene radiocarbon ages associated with *Carnegiea gigantea* and *Encelia farinosa* in other northeastern Sonoran Desert midden studies (Van Devender et al. 1985; Van Devender 1990; Anderson and Van Devender 1991), the few seeds and achenes in WP5 probably represent younger contaminants and not members of the late Wisconsin flora. However, leaflets and seeds of *Prosopis velutina,* a desert grassland dominant, may be contemporaneous considering a radiocarbon date of 11,740 yr B.P. on *P. velutina* mesocarps from a Waterman Mountains midden (Anderson and Van Devender 1991).

The rugged topography and varied microhabitats of Ragged Top have greater potential for the survival of relict populations than nearby larger ranges. Only 24.1% of the 54 taxa in the WP5 sample no longer occur on the mountain. Of the WP5 taxa that still occur on Ragged Top, 53.7% still grow on hot south-facing slopes, including four of five local succulents. Today the south slopes of Wolcott Peak are too hot and dry to support 19 species (46.3%) now restricted to cooler more mesic microhabitats on north slopes and in riparian drainages. The relict plants include shrubs (*Eriogonum fasciculatum, Quercus turbinella, Vauquelinia californica*), a succulent (*Opuntia chlorotica*), grasses (*Bromus carinatus, Stipa speciosa*), perennial herbs (*Ambrosia confertiflora, Physalis crassifolia, Tragia nepetaefolia*), and annuals (*Boerhavia wrightii, Galium aparine, Kallstoemia* spp., and *Plagiobothrys arizonicus*). The relict *Q. turbinella* population contains eight mature plants. *Stipa speciosa* (desert needlegrass) is restricted to a few rocky outcrops on the north side. *Digitaria cognata* (Schult.) Pilg. (fall witchgrass) was only found in a wash on Wolcott Peak.

Overall, the responses of the plants in the Ragged Top flora to Holocene climate changes were modest. The plants that no longer live on Ragged Top represented only 19.2% of the midden flora, but included important structural components in late Wisconsin communities; i.e., trees, shrubs, and large succulents. The distances and directions to their nearest modern populations are of special biogeographical interest. Five species (6.5%) are found on nearby ranges within five kilometers. Another five species can be found on ranges within 40 kilometers. Only four species (5.5%) occur further away (90–135 km).

The absences of the succulents *Agave deserti* and *Ferocactus cylindraceus* (Engelm.) Orcutt (California barrel cactus) on Ragged Top are not easily explained. *Ferocactus cylindraceus* is found as low as 700 m elevation on most of the nearby desert peaks and hills including the Samaniego Hills (4.5 km NE). *Agave deserti* is still found in the Waterman Mountains in a variety of habitats from north-facing granitic slopes to south-facing xeric limestone. The absence of the widespread *Artemisia ludoviciana* (white sage, estafiate) is surprising considering its leaves in the WP5 sample, suitable shady niches on Ragged Top, and extensive populations on the north-facing slopes on the upper elevations of the Silver Bell Mountains (3.5 km S).

The remaining extralocal taxa all occur within 140 km. *Opuntia whipplei* (Whipple cholla) is reported from near Oracle (90 km ENE) but is more typically found in the northern half of Arizona (Benson 1982). A single *Juniperus erythrocarpa* (as *J. monosperma*) reported in the Silver Bell Mountains (3.5 km S; Brown 1978) has not been relocated. Otherwise, the nearest *J. erythrocarpa* occurs as relict populations on Newman Peak in the Picacho Mountains (35 km NNE; Brown 1978). *Pinus monophylla* can be found as close as the Pinal Mountains near Miami (110 km NNE) and on Table Mountain above Aravaipa Canyon (110 km ENE). The most distant of all the identified extralocal species is probably *J. osteosperma,* found as close as the Apache Mountains near Globe (135 km NNE; Little 1971). A specimen from between Vail and Saguaro National Monument (80 km ESE) in the University of Arizona Herbarium was annotated to *J. osteosperma* by Robert P. Adams in 1975. We feel that the identification or the locality is incorrect because *J. erythrocarpa* was the only species reported in the area by Bowers and McLaughlin (1987) in their extensive flora of the nearby Rincon Mountains.

Associations of two or more plants in late Wisconsin woodlands that cannot be found today or are limited to small ecotonal areas today have been reported in several Arizona Upland midden studies, including the nearby Waterman Mountains (Van Devender 1990). Contamination in the Wolcott Peak middens limited inferences of paleoassociations to obvious extralocal woodland/chaparral and winter-rainfall desertscrub taxa. In these assemblages the apparent associations of *Agave deserti* with *Juniperus osteosperma, Opuntia whipplei,* and *Pinus monophylla* appear to be anomalous. The ranges of *A. deserti, J. erythrocarpa,* and *Vauquelinia californica* only overlap in the upper portions of the Ajo Mountains in Organ Pipe Cactus National Monument (110 km WSW; Bowers 1980).

The percentage of trees and woody shrubs (20.4%) in WP5 is nearly twice that of Wolcott Peak (10.6%) and Ragged Top (11.2%) today while herbaceous perennials have been relatively constant (ca. 13%)

over time. However, the low semi-woody plants, here termed subshrubs, increased over two-fold although combined perennial nonsucculents remained relatively constant: late Wisconsin = 40.7%, middle Holocene = 36.4%, Wolcott Peak flora = 41.8%, Ragged Top flora 39.4%. Percentages of woody perennials similar to those in the late Wisconsin Wolcott Peak woodland assemblages were found in four Waterman Mountains samples dated at 11,510 to 12,690 yr B.P. (44.7%; Anderson and Van Devender, 1991) and in two Picacho Peak (25 km NNE) samples dated at 11,100 to 13,170 yr B.P. (38.7%; Van Devender et al. 1991). In contrast, grasses and succulents were better represented in the Ragged Top flora in the late Wisconsin than today.

Middle Holocene. The WP4 sample yielded remains of a Sonoran desertscrub at a rocky cliff base at 5350 yr B.P. The plant assemblage was depauperate because of small sample size and the unusual abundance of bones (Van Devender and Mead 1978; Mead et al. 1983). Twigs of *Juniperus erythrocarpa/monosperma* in the sample were probably contaminants older than 8900 yr B.P. (Van Devender 1990) although rugged topography may have allowed a relict population to survive on Ragged Top later in the Holocene than in other ranges. Several plants sampled including *Celtis pallida, Ericameria laricifolia* (turpentine bush), *Opuntia chlorotica,* and *O. phaeacantha* (variable prickly pear) still occur on Wolcott Peak but not at the midden site, indicating more favorable moisture conditions than today.

A number of desertscrub or subtropical species that are fairly intolerant of freezes and cool, dry summers in the mixed WP2 assemblage were likely associated with the 5020 yr B.P. date rather than the late Wisconsin 14,550 yr B.P. date. They include shrubs (*Celtis pallida, Prosopis velutina*), subshrubs (*Brickellia* cf. *coulteri, Carlowrightia arizonica, Plumbago scandens*), a perennial vine (*Janusia gracilis*), and herbs (*Allionia incarnata, Boerhavia erecta* var. *intermedia, Nicotiana trigonophylla*). *Allionia incarnata, Janusia gracilis,* and *Prosopis velutina* are present elsewhere on Wolcott Peak or Ragged Top but no longer occur near the midden site. *Celtis pallida* appears to have been more common in the past than it is today. Indicators of greater moisture in middle Holocene assemblages are in agreement with previous climatic reconstructions for the Sonoran Desert of summer temperatures greater than today, strong summer monsoons, and reduced winter rainfall (Van Devender et al. 1987; Van Devender 1990).

Previous Sonoran Desert midden studies inferred that more frequent freezes in the middle Holocene than today delayed the northward dispersal of important subtropical Sonoran Desert plants (Van Devender 1990). A number of trees and shrubs not found in the

Wolcott Peak middens are common near the sites today including *Cercidium microphyllum, Horsfordia newberryi, Hyptis emoryi, Larrea divaricata, Olneya tesota,* and *Simmondsia chinensis.* Their arrivals in the area or increases in abundance reflect late Holocene changes in the flora and vegetation in the last 4000 years.

Relict species. The modern climatic and vegetation regimes of Ragged Top were apparently established some time after 5000 years ago. The flora of Ragged Top is exceptionally rich for its elevation, size, and rock types. The richness is primarily due to a great variety of microhabitats allowing many species to live in a small area. The steep, shady cliffs and canyons also provide safe sites for relict populations extirpated from more exposed areas in the region. The packrat middens provide evidence that the Ragged Top relicts were isolated at different times. *Quercus turbinella, Vauquelinia californica,* and *Yucca baccata* are chaparral/woodland plants that were more widespread prior to 8900 years ago. Brown (1978) summarized isolated populations of relict plants including these species, *Juniperus erythrocarpa,* and *Rhus aromatica* in 22 desert mountain ranges in Arizona. A small population of *Ipomopsis multiflora* on Ragged Top may have been isolated at the same time. Other relictual populations of species that occurred more widely in the Wisconsin and are common in woodland and chaparral today include *Y. baccata* in the Silver Bell (3.5 km S) Mountains, *Agave deserti* and *Y. baccata* in the Waterman Mountains (10 km S), *Morus microphylla* (Texas mulberry), *R. aromatica, Q. turbinella, V. californica,* and *Y. baccata* in the Tucson Mountains (35 km SE), and *Agave palmeri* (Palmer agave), and *M. microphylla, Q. turbinella, V. californica* in the Picacho (35 km NNE) Mountains. We have seen no evidence of genetic changes in these populations after 9000 years of isolation.

Other Ragged Top relicts such as *Echinopepon wrightii* (wild balsam apple), *Ipomoea cristulata* Hallier f. (scarlet morning glory), and *Pisonia capitata* (Wats.) Standl. (garumbullo) are more topical, summer rainfall plants which probably reached the area between 4000 and 8900 years ago. The latter is a tropical shrub in the Nyctaginaceae disjunct from the nearest Sonoran populations by 460 kilometers (Wiens 1990). A single colony of four female plants is in a narrow, shady crevice. Other subtropical relicts whose dispersal and isolation probably dates to the middle or late Holocene include *Coursetia glandulosa* Gray (baby bonnets) on Pan Quemado (12 km SSE) and Ragged Top, and *Stenocereus thurberi* (Engelm.) Gibson & Horak on Desert Peak (34 km NE; Benson, 1982) and in the Roskruge Mountains (24 km S: 1.8 mi. NW Pescadero Mountain, T14S R9E S9, NW¼, 825 m elev.; S. Norman personal communication 1991). Pollen and seeds of *Bursera* in packrat middens record the arrivals of *Bursera* aff. *microphylla* (elephant tree) in the Wa-

terman Mountains by 5190 yr B.P. (Anderson and Van Devender 1991).

The middens also indicate that the abundances of plants in the modern desertscrub community on Wolcott Peak have increased and decreased, and local distributions have shifted in the last 5000 years. Studies of more continuous Holocene midden sequences from the Sonoran Desert suggest that community composition and structure have varied continuously without approaching equilibria in response to climate changes on time scales from millennia to decades (Van Devender et al. 1987; Anderson and Van Devender 1991; Van Devender 1990).

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